A Quantitative Analysis of the Growth of Helianthus annuus. Part I.—*The Respiration of the Plant and of its Parts throughout the Life Cycle.*

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CONTENTS.

		PAGE
1.	Introduction	368
2.	The Respiratory Index as a Measure of the Effect of the "Internal" Factor upon the Rate of Respiration	369
3.	Material and Methods	370
4.	Experiments to Determine the Relation between Temperature and Respiration, and a Suitable Temperature at which to Determine the Respiratory Index	371
5.	The Decrease with Age in the Respiratory Index of the Plant and of its Parts	375
6.	Respiration of Uncut Plants in the Field	379
7.	The Relation of the Respiratory Index to Relative Growth Rate	381
8.	Summary	383

1. *Introduction.*

By means of a quantitative analysis of plant growth we attempt to apportion the external and internal influences that determine the course of a plant's development. The former can be analysed as various recognised environmental factors, the latter at present may be grouped together as the "internal" factor for growth. The general methods formulated for such an analysis have been outlined in a previous paper (8). In the present series of papers, of which this is the first, an account is given of such an analysis of the growth of *Helianthus annuus*. The present paper is mainly confined to an account of the results obtained in an experimental study of the respiration of *Helianthus annuus* throughout its life cycle. As far as the authors are aware such a study of the respiration of a plant throughout its life cycle has not before been carried out.

The method has been to determine at frequent intervals throughout the life cycle, the respiration at a given constant temperature of a representative plant of a crop. From these results it is possible to estimate the respiration of a mean plant of the crop at the recorded fluctuating temperature of the field and so to obtain a measure of the rate of loss in dry-weight of the plant.

under field conditions. In addition, the results afford information as to the effect of age upon respiration. Furthermore, it is thus possible to compare the effect of progressing age upon the rate of respiration with the effect of age upon the relative rate of increase in dry-weight.

For each plant process or group of processes, such as respiration or growth, there is a group of factors within the plant which will affect the rate of the particular process or group of processes. Each group we will call the "internal" factor for that process, it being clearly understood that groups may have factors in common or may even be identical. This quantitative study of plant growth may enable one to elucidate the interconnection of these "internal" factors.

2. *The Respiratory Index as a Measure of the Effect of the "Internal" Factor upon the Rate of Respiration.*

In any attempt to determine the effect of the "internal" factor upon the rate of respiration throughout the life cycle of the plant the other factors affecting respiration should be standardised, that is, kept constant or not limiting throughout the experiments.

In view of our present knowledge of respiration the factors which may affect the rate of respiration per unit of dry-weight* can be classified as follows:—

1. Concentration of respirable material.
2. Effective amount of respiring cell-matter per unit of dry-weight. This we term the "internal" factor for respiration.
3. Concentration of oxygen.
4. Temperature.

Our measurements of respiration have been made per gramme dry-weight. In order to make the results strictly comparable from the point of view of the "internal" factor, the respiration should be measured when the amount of respirable material is in excess, the internal concentration of oxygen constant and the temperature at a definite constant value. Under such conditions the respiration per gramme dry-weight will be a measure, for purposes of comparison from time to time, of the effective amount of respiring cell-matter per gramme dry-weight, that is to say, of the "internal" factor.

It has been generally assumed that the concentration of oxygen in the atmosphere (*i.e.*, about 21 per cent.) provides an excess of oxygen for respiration. Recent work in this laboratory has shown that such is not the case, but that the carbon dioxide output,* starting from low pressures of oxygen in the atmosphere, increases with rising partial pressures, at first rapidly and then more and more slowly until a maximum is reached, and then decreases. The position of this maximum will presumably depend upon the permeability of the tissue to oxygen, the internal concentration of oxygen being the important factor. Although experiments have not been carried out with *Helianthus,* the results obtained with similar tissues of other plants indicate that an external concentration of 21 per cent. is sub-maximal, but variations in the concentration in this region only slightly affect the rate of carbon dioxide production. We have assumed that in using a constant external concentration of oxygen we have been getting a close approximation to a constant internal concentration, and therefore in view of what has been said above, that the results will be comparable.

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* Having already decided to express growth per unit of dry-weight, it is necessary to use the same unit when dealing with respiration, in order to make the results comparable.

With regard to the concentration of respirable material, if the rate of respiration remains constant, other factors being constant, it is probably safe to assume that the concentration of respirable material is in excess. Respiration expressed per gramme dry-weight per hour, when measured with the respirable material in excess, with the external concentration of oxygen that of the atmosphere, and with the temperature at 10° C., we propose to call the respiratory index, and from what we have said above, the respiratory index may be taken as a measure of the effective amount of respiring cell-matter per gramme dry-weight, or in other words, a measure of the "internal" factor.†

3. *Material and Methods.*

A detailed account of the plants used and of the manner in which they were grown will appear in the further papers of this series. In the present communication it will suffice to state that the variety of *Helianthus annuus* used was Sutton's "Giant Yellow" and that the plants were grown in the field under natural conditions of illumination and temperature and under optimal conditions of spacing and soil humidity. The seeds were sown on May 22, 1920, and the seedlings appeared above the surface on the 27th. While the plants were small the output of carbon dioxide was determined by absorption with baryta in Pettenkofer tubes, but later in the case of the larger plants the carbon dioxide was absorbed by NaOH in Reiset towers. The plants were cut off at the level of the ground. The plants used for respiration determinations were gathered towards the end of the day so that they should be taken after a period of active assimilation. Sufficient time was allowed for the tissue to cool down to the temperature of the respiration chamber. Whilst the plants were cooling down air deprived of carbon dioxide were drawn over at the same rate as that at which it was to be carried over during the experiment. The vessels used were always as small as the size of the material would permit in order that the time interval between the evolution of carbon dioxide from the tissues and its absorption by the baryta or soda should be minimal and that the current necessary to keep the carbon dioxide-content of the air in the vessel low should not be excessive. To this end it was found very suitable to enclose the plant material in a flexible air-proof fabric, since a covering of such a fabric collapses when air is drawn through it and clings tightly to the plant material. Until the plants were about 10 grm. in weight they were used entire, but subsequently the respiration of the stem, leaves and flowers was measured separately.

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* In the absence of any deeper knowledge of the process of respiration, the rate of carbon dioxide production is employed as a measure of the rate of the process.

† Palladin (7) has shown for seedlings that the respiration under constant external conditions, when carbohydrate is in excess, is proportional to the fraction of protein which is unattacked by gastric juice, thus suggesting that the amount of nuclein nitrogen is a measure of the amount of respiring cell-matter. This suggests that the respiratory index of the plant may be related to its nuclein nitrogen-content.

4. *Experiments to Determine the Relation between Temperature and Respiration, and a Suitable Temperature at which to Determine the Respiratory Index.*

It is known that at high temperatures the rate of respiration of plant tissues decreases after a short interval. This falling off in the rate of respiration has been attributed to a decrease in the effective amount of respiring cell-matter due to the high temperature ("time factor" of Blackman). The result may, nevertheless, in some cases be due to a decrease in concentration of respirable material with time. At medium and low temperatures it has been shown by Kuyper (5) for seedlings, and in this laboratory for leaves, that the respiration remains constant for an appreciable interval of time after separating a tissue from its source of carbohydrate supply.

With these considerations in view, a series of preliminary experiments was conducted to investigate the respiration of cut plants of *Helianthus* at various temperatures in order to ascertain for what length of time, after gathering, the respiration remained constant. The results provide at the same time data for the construction of a temperature-respiration curve.

Experiments were carried out with plants while young, *i.e.*, before the fourth pair of leaves had begun to develop. During this period, as will be shown later, the respiratory index changes little with age. Constant temperature rooms at low, medium, and high temperatures were utilised. The results are presented in Tables I to III and figs. 1 and 2.

Table I.—Respiration of *Helianthus annuus* at Low Temperatures.

No. of experiment.	Days from germination.	Interval between gathering and placing in temperature chamber.	Time in temperature chamber before estimations started.	No. of plants used.	Dry-weight of an average plant.	Temperature during experiment.	Duration of experiment.	Respiration (Mgrm. CO_2 per gramme dry-weight per hour).
		hours.	hours.		mgrm.	° C.	hours.	
1	12	2·5	6	20	197	3·5	41·2	1·28
2	14	0·75	2	12	184	1·8	15·2	1·042
3	15	0·5	4·75	10	180	1·0	14·6	0·97

With regard to the respiration at 25° C., it will be seen that the rate falls continuously after the first period of measurement, and that, as far as our results show, the initial rate of respiration can only be determined approximately at this temperature by extrapolating the curve. In estimating the initial rate of respiration at 25° C., we have assumed that the falling off has been continuous. At 10° C. no falling off occurred for about twelve hours. After this period the rate of respiration falls off, as is shown in Table II, Experiment 3. Presumably, in the case of older plants, where the amount of respirable material relative to respiring cell-matter is greater, the period before the falling off commences would be longer, and such was actually observed. Having found that at 10° C. there is no falling off for several hours in the rate of respiration, we have used that temperature throughout and have adopted it as the standard temperature of the respiratory index. It will be seen later that the index may range from 3·0 to 0·08 for different parts and ages of the plant.

At this point, the evidence which justifies the application of the temperature-respiration relation to the calculation of the respiration under the conditions of fluctuating temperature obtaining in the field may be considered.

At an early stage in the life of the plant, the actual respiration at the fluctuating temperature obtaining in the field was determined continuously for eight days (June 10, 1920, to June 18, 1920), fresh plants being used every half day.

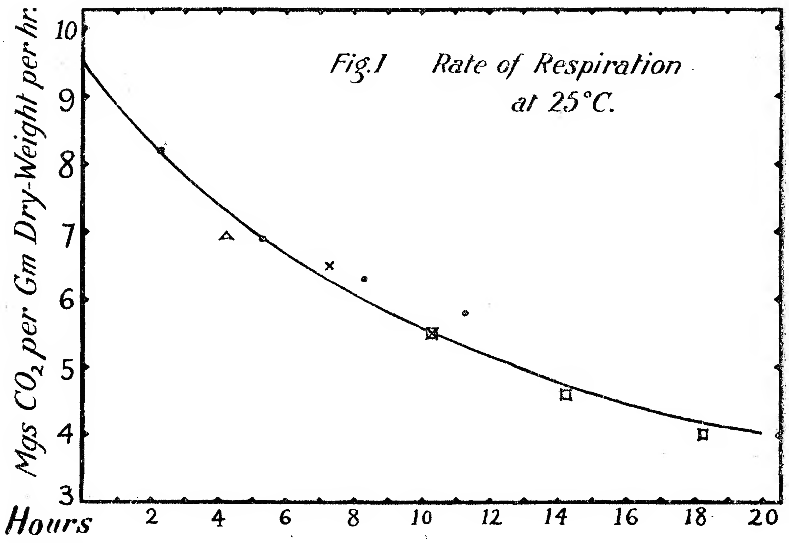
The results of these determinations of the actual respiration were

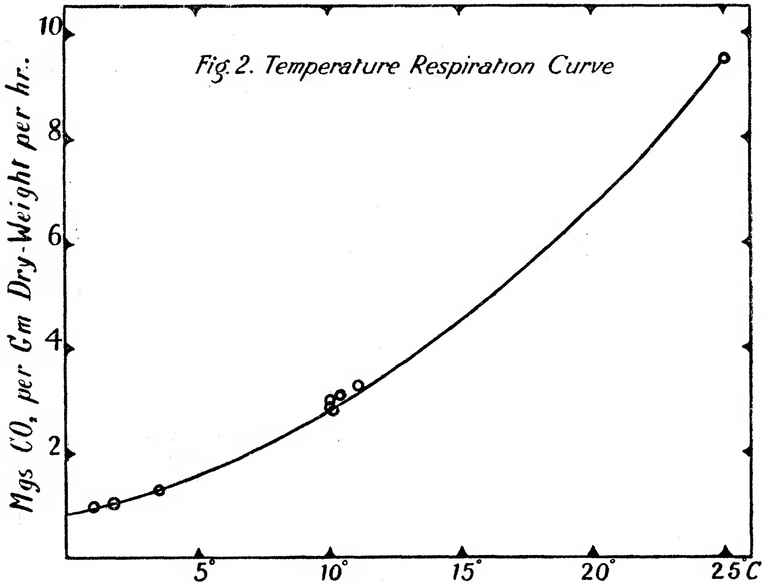
Table II.—Respiration of *Helianthus annuus* at Medium Temperatures.

No. of experiment.	Days from germination.	Interval between gathering and placing in temperature chamber.	Time in temperature chamber before estimations started.	No. of plants used.	Dry-weight of an average plant.	Respiration (Mgrm. CO_2 per gramme dry-weight per hour).
		hours.	hours.		mgrm.	
1	1	0·25	2	30	22·5	3 hrs. at 10° C. 3 hrs. at 10° C. 2·9 → 2·8
2	2	0·75	3·5	25	22·3	13·5 hrs. at 10·4° C. 3·1
3	4	0·25	3	25	24·2	3 hrs. at 10° C. 17 hrs. at 10° C. 3·0 → 2·1
4	12	0·5	4·3	10	101	4 hrs. at 10·2°. 3½ hrs. at 10·1°. 6 hrs. at 9·9°. 2·7 → 2·8 → 2·5
5	21	0·5	3·25	8	630	2 hrs. at 11·1° 2 hrs. at 11·2°. 2 hrs. at 11·3°. 2 hrs. at 11·4°. 3·3 → 3·2 → 3·4 → 3·3

Table III.—Respiration of *Helianthus annuus* at High Temperatures.

No. of experiment.	Days from germination.	Interval between gathering and placing in temperature chamber.	Time in temperature chamber before estimations started.	No. of plants used.	Dry-weight of an average plant.	Temperature during experiment.	Respiration (Mgrm. CO_2 per gramme dry-weight per hour).
		hours.	hours.		mgrm.	° C.	
1	11	2·5	3	40	175	25	2½ hrs. 6·9
2	14	0·75	5·8	10	163	25	3 hrs. 3 hrs. 6·5 → 5·5
3	15	0·5	8·25	10	157	25	4 hrs. 4 hrs. 4 hrs. 5·5 → 4·6 → 4·0
4	18	0·5	0·8	4	485	25	3 hrs. 3 hrs. 3 hrs. 3 hrs. 8·2 → 6·9 → 6·3 → 5·8





compared with values calculated from the respiratory index determined at 10° C. on one occasion during the eight days. For the purpose of this calculation, the physiological mean temperature for each period was found from the temperature record.* Our method of obtaining this is as follows.

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* There are several possible methods of obtaining the average temperature for a period. The geometric mean temperature would be used in preference to the arithmetic mean temperature, because the rate of a physiological process is not a linear function of temperature. But since the temperature coefficient decreases with increase of temperature it is not sufficiently correct to use a geometric mean.

The recorded temperatures—in our case taken at hourly intervals—are tabulated. For each temperature, the rate of the reaction (*i.e.*, respiration) is obtained from the temperature-respiration curve. The arithmetic mean of these is taken, and the corresponding temperature obtained from the temperature-respiration curve.

The total observed production of carbon dioxide was 299 mgrm., whilst the calculated value was 326 mgrm. This agreement is good, considering the fact that a falling off in the rate of respiration must have occurred during the periods when high temperatures obtained. The results of the experiment, as a whole, show that a satisfactory allowance for fluctuating temperature can be made by means of the temperature-respiration curve, at least during the earlier stages of the life-cycle, to which the above experiment applies.

5. *The Decrease with Age in the Respiratory Index of the Plant and of its Parts.*

We may now proceed to the main issue, namely, the determination of the respiratory index of the whole plant and of its parts throughout the life-cycle.

The results of the actual experiments are given in Table IV.

Table IV.—Observed Respiratory Index of Plants of Different Age.

Days from germination.	Number of plants used.	Dry-weight of a single plant.	Respiratory index (mgrm. CO_2 per gramme dry-weight per hour) of				Total inflorescences.	Flowers on lateral shoots.
			Entire plant.	Stem.	Leaves.	Stem-apex.		
		grm.						
1	30	0·0225	2·90					
2	25	0·0223	3·00					
4	25	0·0242	3·00					
13	10	0·1009	2·80					
22	8	0·630	3·00	(3·00)	(3·00)	3·00		
29	2	4·065	2·30					
36	1	12·85	1·21	0·81	1·56			
43	1	22·05	1·03	0·69	1·38			
50	1	45·15	0·94	0·46	1·52	2·56		
59	1	93·20	0·66	0·33	1·32	1·72		
64	1	98·30	0·71	0·34	1·24			
89	1	294·7	0·48	6·31	0·90	1·13*	1·13	
99	1	377·4	0·37	0·25	0·45	0·89	1·04	1·31
112	1	818·3	0·26	0·098	0·375	0·75	0·85	0·95
136	1	419·5	0·39	0·081	0·44	0·96	0·965	0·97

* From this date onwards the stem-apex was the inflorescence only.

In the first place, with regard to the plant as a whole, in applying these results for the purpose for which they were intended, namely, for determining variations with age in the value of the respiratory index and for calculating the respiration in the field of a mean plant, the objection may be raised that no allowance is made for the probable error of the respiration value determined from a single plant. It is true that it would have been better to have determined simultaneously the respiration of several individual plants, and from the results obtained to have calculated the mean result with its probable error. Such a procedure was impossible with the facilities at our disposal. We can, however, apply the following correction to our figures. Probably a principal cause of any extensive difference between the respiratory index of one plant and that of another is the difference in the relative proportion of stem to leaf, when the respiration of the stem differs from that of the leaves. Knowing the difference between the relative proportion of stem to leaf in the plant used for determining the respiration and that in a mean plant, and having after the thirty-fourth day from germination determined the respiration of the stem and leaves separately, we have from this date onwards been able to make an allowance for the effect of a difference in proportion of stem to leaf in calculating the respiratory index of a mean plant. This correction, however, makes very little difference. The figures for the respiratory index of a mean plant of the harvest are given in Table 5.

Table V.—Calculated Respiratory Index of an Average Harvested Plant.

Days from germination.	Dry-weight of plant.	Respiration per hour at 10° C. of an average plant.	Respiratory index of an average plant (mgrm. CO_2 per gramme dry-weight per hour).
	grm.	mgrm. CO_2.	
1	0·0238	0·071	2·9
8	0·0707	0·212	2·9
22	1·128	3·38	3·0
29	4·53	10·4	2·3
36	12·35	14·9	1·2
43	26·9	27·7	1·03
50	60·1	56·1	0·93
57	92·8	68·8	0·74
64	133	91·5	0·69
85	352	176	0·53
99	559	198	0·35
113	765	233	0·31
127	873	345	0·39

It will be seen from the above Table that the value for the respiratory index of the mean plant falls off continuously from 3 to about one-tenth of that amount at the end of the life-cycle.

When in the second place we consider the respiration of the various parts of a plant, such as the stem, leaves, and flowers, we find a similar phenomenon of a decrease in the respiratory index with age. Table IV shows a fall in the value of the respiratory index of the stem from 0·8 on the thirty-sixth day from germination to 0·08 on the 136th day from germination, and, in the value of all the leaves taken together, from 1·56 to 0·44.

Table VI.—Respiration of Leaves of *Helianthus annuus.*

Days from germination.	Description of leaves used.	Number of leaves used.	Weight of leaves used.	Weight of an individual leaf.	Respiratory index (mgrm. CO_2 per grm. dry-weight per hour).
			grm.	grm.	
22	Seedling plant (minus roots)	—	0·630	—	3·00
50	Top cluster and one or two small leaves	—	4·65	—	2·56
	The remaining leaves of the plant	—	16·00	—	1·21
53	Top cluster of leaves: A + flower rudiments	—	4·76	—	1·84
	B − flower rudiments	—	2·64	—	1·80
54	2nd pair from bottom of plant (excluding cotyledons)	12	5·85	0·49	0·89
	3rd pair do.	12	11·35	0·95	0·89
	4th pair do.	12	17·40	1·45	1·00
	5th pair do.	12	21·90	1·83	1·02
	Two pairs next to top cluster	24	23·50	0·98	1·81
	Top cluster (flower rudiments just appearing)	—	11·10	—	1·83
59	Top cluster of leaves (including flower rudiments)	—	3·40	—	1·72
	Remaining leaves of plant	—	27·80	—	1·27
64	Upper (*i.e.* younger) leaves of the plant	—	1·96	—	1·70
	Remaining leaves of plant	—	31·70	—	1·22
89	All the leaves of the plant	—	79·00	—	0·905
99	Leaves off the lateral branches	—	14·70	—	1·11
	Leaves off main stem	—	72·50	—	0·32
112	Leaves off the lateral branches	—	44·50	—	0·60
	Upper leaves off main stem	—	77·90	—	0·365
	Lower leaves off main stem	—	90·50	—	0·27
136	All the leaves of the plant	—	78·50	—	0·44

The decrease in the rate of respiration of all the leaves taken together is undoubtedly an expression of the fact that the respiratory index of individual leaves falls off with age—a fact previously established by Nicolas (6).*

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* Nicolas (6) showed that, broadly speaking, the rate of respiration of leaves is dependent upon their age; but this investigator did not distinguish between the changes in the rate of respiration due to differences in the age of the leaf and those due to differences of the age of the plant.

Inspection of Table VI shows that, on the twenty-second day from germination, the value of the respiratory index of the young plant with three or four pairs of leaves was about 3; on the fifty-fourth day from germination, the values for the second, third, and fourth pairs of leaves (from the bottom of the plant) were 0·89, 0·89, and 1·0 respectively. On the 112th day from germination, on which date the three lowermost pairs of leaves had fallen, the value of the respiratory index of those remaining on the lower half of the stem was only 0·27.

A similar decrease has been observed in the case of the flowers, whether the main inflorescence alone or whether all the flowers of the plant be considered.

We come finally to the results obtained with the actively growing stem-apex. The case here has the peculiar interest that we are dealing with a tissue which, unlike the plant as a whole and the parts previously mentioned, is not complicated by increasing differentiation with age, but is still mainly meristematic and might therefore be expected to retain its original respiratory activity. The respiratory index at the stem-apex is not, as might be expected, constant throughout the life of the plant, but falls continuously as the age of the plant increases. The stem-apex may be regarded as giving us the initial respiratory index of each leaf as it appears; that is, approximately the respiratory index of the meristematic tissue.

In Table VI it is seen that on the twenty-second day from germination the value of the respiratory index of the top cluster of leaves (in this case the entire seedling plant) was 3. On the fiftieth day from germination the value for the respiratory index of the top cluster of leaves was 2·56, whilst on the fifty-ninth day from germination it had fallen to 1·72. After this date the inflorescence appeared, but, as will be seen from the same Table, on the fifty-third day from germination the value for the respiratory index of a top cluster of leaves without visible flower rudiments was the same (1·80) as that for a top cluster of leaves from another plant in which the young inflorescence had developed.

In concluding this section we may consider the decrease with age in the respiratory index of the whole plant with a view to separating the component factors which we have until now grouped together as the "internal" factor. It will be seen from Table IV that during the first fifty-nine days from germination, after which period the inflorescence appeared, the greatest fall in the value of the respiratory index occurs in the case of the stem, whereas the fall is smallest in the case of the stem-apex. If we assume that the value for the respiratory index of the stem, leaves, and stem-apex is the same just after germination—the fact that the respiratory index of the entire plant does not change appreciably for a period extending over more than three weeks from germination being good evidence that this is the case—we find that the fall in the respiratory index during this period of the stem, leaves, and stem-apex is 89, 56, and 43 per cent. of the original value respectively. The fall in the case of the stem and leaves must be partly due to the increasing proportion of definitely non-living tissue, such as mechanical and water-conducting tissues, but this cannot be the explanation of the fall in the respiratory index of the stem-apex. The fact that the respiratory index of the youngest leaves falls with the age of the plant is interesting and calls for an explanation in itself. On our postulates the effective amount of respiring cell-matter per gramme dry-weight in the young leaves becomes smaller as the age of the plant increases. As to whether this is due to a decreasing amount of protoplasm or respiring enzymes per gramme dry-weight, or to an increasing amount of some inhibitor, remains an interesting question, to be answered by further research. It is interesting to note, however, that the photosynthetic activity of the young leaves also falls off with increasing age of the plant.* A knowledge of the protoplasmic nitrogen-content of the whole plant and of its parts, particularly that of the young leaves, would possibly throw light on the causes underlying the fall with age in the respiratory index.

6. *Respiration of Uncut Plants in the Field.*

The following experiments wth uncut plants in the field are of interest in that they confirm the results already described, which were obtained with cut plants in the laboratory. On five occasions, scattered throughout the life-cycle, the respiration of an uncut plant was determined *in situ* in the field. The leaves of the plants were drawn up to the stem and secured with string; an airtight fabric covering was then placed over the plant. This covering was made airtight at the base by means of a waxed joint holding water. The top of the covering was tied and also sealed with wax. The inlet was a long narrow tube at the top, the outlet being at the bottom. A current of air was drawn over the plant and thence through a gas meter. The carbon dioxide was absorbed by caustic soda in a couple of Reiset towers. Allowance was made for the carbon dioxide present in the air at the rate of 3 c.c. per 10 litres. The physiological mean temperature was taken and the respiration results were reduced to 10° C. by means of the temperature-respiration relation previously established. The results are presented in Table VII, in which are also recorded the respiratory indices for the dates in question.

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* Unpublished work by G. E. Briggs.

Table VII.

Dates and times of experiment.	Dry-weight of a single plant.	Physiological mean temperature.	Mgrm. of CO_2 per gramme dry-weight per hour calculated for 10° C.	Respiratory index for mean plant.
	grm.	° C.		
5 P.M., June 26, to 10.5 A.M., June 27	5 ·68	16 ·0	1 ·58	2 ·00
4.20 P.M., July 15, to 7.10 A.M., July 16	51 ·4	12 ·6	1 ·28	0 ·96
4.3 P.M., July 19, to 12.10 P.M., July 20	62 ·5	15 ·3	0 ·94	0 ·97
2.3 P.M., Aug. 17, to 8.26 P.M., Aug. 17	227	16 ·7	0 ·69	0 ·58
7.32 P.M., Sept. 11, to 9.34 A.M., Sept. 12 ...	354	6 ·8	0 ·26	0 ·30

The evidence from uncut plants in the field corroborates that derived from cut plants in the laboratory to the extent that there is continuous falling off in the respiration with age, and, moreover, the values given are of the same order. The agreement is not very close, three being higher and two lower than the respiratory index of the average plant at the same date. In view of the following considerations, a close agreement is not to be expected. Whilst in the case of the laboratory experiments the temperature of the tissues was presumably that of the chamber, since suitable precautions were taken, in the case of the field experiments there must have been a considerable lag before the cooling down or warming up of the bulky tissues was accomplished. Again, whilst in the laboratory the volume of the respiration chamber was minimal, the airtight fabric collapsing closely round the plant tissue, such a condition was impossible in the field without unduly damaging the plants. Further, by tying the leaves up they were subjected to a continuous geotropic stimulus, which was exhibited when the plants were untied by a decided downward movement of the leaves, which took up a fixed position with the petioles pointing almost vertically downwards. Another possible source of error attaching to the field experiments lies in a possible inaccuracy in the allowance made for the carbon dioxide-content of the air; but this, however, could only slightly affect the results. Finally, the proportion of leaf to stem was not that of a mean plant and could not be allowed for, since the respiration of the leaves and stem could not be determined separately.

7. *The Relation of the Respiratory Index to Relative Growth Rate.*

The relative growth rate, which we have elsewhere (8)* termed R., is the average rate of increase in dry-weight per unit dry-weight per week (expressed as a percentage). In previous papers (1 and 4) we have shown that the relative growth rate appears to vary with age in a manner slightly different for different plants, but to be always characterised by a fall beginning at an early period in the life cycle; this fall is very similar to the fall which we have recorded above in the values of the respiratory index of *Helianthus annuus.* In the present research we can make a direct comparison between the respiratory index, which is the rate of respiration per unit dry-weight, and R., since we have the results for the relative growth rates of the same crop of plants as that used for determining the respiration. The comparison is represented in fig. 3 and Table VIII. Fig. 3 shows three curves:—The relative growth rate values, the values for the respiratory index and the values for the respiratory activity at the average temperature obtaining in the field, that is, the respiratory index corrected to the average temperature in the field by means of the temperature-respiration relationship established above, plotted in each case against days from germination. Table VIII also gives the ratios of relative growth rate to the respiratory index and to the respiratory activity at the average temperature obtaining in the field.

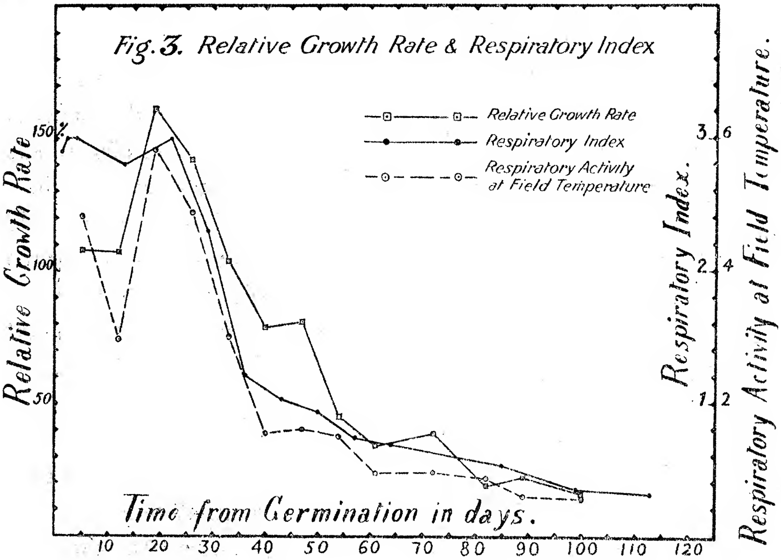

Fig. 3. Relative Growth Rate & Respiratory Index

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* $\frac{R}{100} = \log_e W_2 - \log_e W_1$, where W_2 and W_1 are the dry-weights at the end and beginning of the week respectively, and e the base of the natural logarithms.

Table VIII.—Relation between Growth Rate and Respiratory Activity.

Days from germination.	Relative growth rates.	Respiratory index.	Ratio of relative growth rate to respiratory index.	Respiratory activity at average field temperature.	Ratio of relative growth rate to respiratory activity at average field temperature.	Physiological mean temperature in the field.
5	108	2·97	0·365	4·85	0·223	15·1
12	107	2·82	0·38	2·97	0·360	10·5
19	161	2·92	0·55	5·84	0·275	17·6
26	142	2·60	0·55	4·87	0·291	16·8
33	104	1·65	0·63	3·09	0·336	16·6
40	79	1·10	0·72	1·58	0·500	13·6
47	81	0·97	0·84	1·63	0·496	15·4
54	45	0·82	0·55	1·52	0·296	16·6
61	34	0·72	0·47	0·94	0·361	12·8
72	39	0·63	0·62	0·97	0·402	14·4
82	19	0·53	0·36	0·90	0·211	15·1
89	22	0·47	0·47	0·62	0·355	12·5
100	16	0·38	0·42	0·52	0·308	14·0
114	4·5	0·32	0·14			

It will be seen that while the relative growth rates vary over a wide range, the ratio of the relative growth rate to the respiratory index remains fairly constant throughout the life-cycle. In considering these ratios it should be borne in mind that the values for the respiratory index and for the relative growth rate are not strictly comparable for the following reason. Whereas the values for the respiratory activity are maximal values for the temperature, whether 10° C. or the average temperature of the field, the values for the relative growth rate may not be, but may be limited by the operation of uncontrolled factors, such for example as supply of carbohydrate or of inorganic salts.

In order to be strictly comparable, whether *inter se* or with the respiratory activity, the values of the relative growth rate should be maximal, that is, not limited. Further, the respiratory activity and the relative growth rate, both being maximal at field temperatures, would be comparable throughout the life cycle only if the effect of temperature upon the relative growth rate and upon the respiratory activity were the same. In other words, for purposes of strict comparison the respiratory activity and the relative growth rate should not only both be maximal values but should both be determined at the same constant temperature throughout the life-cycle. Since we do not know the relation between temperature and growth the legitimacy of correcting the respiratory index values determined at 10° C. up to field temperatures for comparison with the relative growth rate is doubtful. As a result of this correction, however, the ratio of relative growth rate to respiratory activity at field temperatures is seen to vary with one exception inversely with temperature. In view of this and of the fact that the correlation coefficient of this ratio with temperature is −0·34, it would seem either that the relative growth rate (when not limited by such factors as carbohydrate or salt supply) has a lower temperature coefficient than respiration, or that the relative growth rates at higher temperatures are limited by some factor.

In view of the close relation between the respiratory index and nuclein nitrogen, as established by Palladin (7), on the one hand, and that between the respiratory index and the relative growth rate, as demonstrated above, on the other, one would expect the growth rate to be intimately connected with the concentration of nuclein nitrogen per gramme dry-weight. It must be realised, however, that whereas the first relation was established for wheat, the second was established for *Helianthus annuus.*

The only type of evidence available with regard to the third suggested relation is that provided by the results obtained by Hornberger (3), who determined the protein nitrogen-content of maize. These results are for the same plants as those for which we have already calculated the relative growth rate (1). The growth per protein nitrogen for successive weeks, which we have calculated, is as follows:—

Grammes dry-weight per gramme Nitrogen per Week.

22·0	32·4
42·5	20·0
25·9	15·2
27·7	16·2
38·1	27·5

As to the relation of nuclein nitrogen to protein nitrogen we at present have no evidence.

It is proposed to reserve further consideration of the relation between respiration and growth until we have presented the growth data in full.

8. *Summary.*

The respiratory index has been defined as the respiration determined per gramme dry-weight per hour at 10° C. when the amount of respirable material is not limiting and when the external concentration of oxygen is that of the atmosphere. The respiratory index is consequently a measure of the effective amount of respiring cell-matter per gramme dry-weight, that is the "internal" factor for respiration.

The respiratory index of the entire plant falls off continuously from 3 to about one-tenth of this value at the end of the life-cycle. The respiratory index of the stem of individual leaves and of the flowers respectively

decreases with the age of the organ. The initial respiratory index of successive leaves—*i.e.*, the respiratory index of the stem-apex—decreases with the age of the plant, indicating that the respiratory index of the meristematic tissue decreases with age. The fall in the respiratory index of the meristematic tissue and young leaves shows that the fall in the respiratory index of the whole plant is not, as might be expected, due entirely to the increase in proportion of such tissues as mechanical and water-conducting tissue.

The fall in the value of the respiratory index with age follows closely that in the value of the relative growth rate, thus indicating a close connection between the "internal" factor for respiration and the "internal" factor for growth.

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